

Patterns of Larval Settlement are not Predictable from Coarse Measures of Surface Circulation

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Abstract

We measured settlement of larval invertebrates at 5 intertidal sites and 8 subtidal sites in the San Juan Archipelago from February through August, 2001, and estimated species richness of epibenthic assemblages at 15 intertidal sites in the same region. We compared our results with rates of particle accumulation as evidenced by prior drift card studies. We found no significant positive correlation between particle accumulation, intensity of larval settlement, or species richness. These results indicate that rates of particle accumulation cannot be used as a surrogate for larval settlement or species richness at spatial scales of 1-10 km, and that larval behavior and post-settlement processes are likely to substantially influence patterns of settlement and species richness at these scales. These results are discussed in the context of regional marine reserve network design.

Introduction

Marine protected areas (MPAs) and marine reserves (MRs) are likely to be most effective in sustaining viable populations of benthic organisms when established as networks of sites linked through larval dispersal (e.g., Allison et al. 1996, Roberts et al. 2003). This expectation is based on the assumption that local population persistence will be enhanced through larval immigration into, and emigration from, protected areas. The design of functional networks therefore requires that larval linkages between sites be reasonably likely. However, in the context of MR network planning, it is not feasible to determine the probability of site-specific larval linkages for all taxa, or across all temporal and spatial scales of interest. Consequently, the development of reliable and feasible surrogates for larval exchange that can be applied across relevant taxonomic, spatial, and temporal scales could help to identify high-value sites for purposes of reserve siting and MR network planning.

We tested whether indicators of local surface circulation, specifically Lagrangian transport and particle accumulation, could provide a useful surrogate for patterns of larval settlement in the San Juan Archipelago, Washington. Larval settlement reflects only the potential for immigration to a site, and ignores the potential for emigration from a site. We therefore stress that our data cannot be used to address emigration. Even so, a method that facilitates identification of sites likely to sustain high levels of larval settlement has potential benefit to network design.

We further tested whether particle accumulation was correlated with patterns of species richness within intertidal epibenthic assemblages. We hypothesized that sites experiencing consistently high levels of particle accumulation would accumulate more species than sites experiencing low levels of particle accumulation. This hypothesis unrealistically ignores the importance of post-settlement processes in determining species richness within sites. Even so, it allows us to test the utility of particle accumulation as a surrogate for larval settlement and species richness over longer temporal scales than allowed by instantaneous measure of settlement alone.

Methods

Larval settlement studies. We used results from a drift card study conducted in 1999-2000 (Klinger and Ebbesmeyer 2001) to identify sites exhibiting low, intermediate, and high levels of particle accumulation. From these, we chose 5 intertidal sites and 8 subtidal sites at which to sample invertebrate larval settlement. All sites were located in San Juan Channel between Wasp Passage and Cattle Pass. The northernmost and southernmost sites were separated by a linear distance of about 12 km; individual sites were separated by a distance of at least 1 km. Sites were matched as closely as possible for substrate type, relief, and elevation (intertidal sites) or depth (subtidal sites).

At intertidal sites, we deployed larval traps modeled after those used by Castilla (1998), with the modification that we used no killing agents in the traps. Three replicate traps were deployed repeatedly at each of 5 sites. Traps were deployed fortnightly at the commencement of spring and neap tide periods from June through August, 2001, and were retrieved after 3 days (pilot studies showed that larval mortality due to predation within the traps was negligible from 1-3 days, but increased after 4 days). The contents of each trap were identified according to taxonomic group and larval stage, and counted.

At subtidal sites, we deployed larval traps modeled after those used by other researchers to trap crustaceans, echinoderms, and other invertebrate larvae (e.g., Wing et al. 1995). Each trap consisted of two nylon-bristle scrub brushes (6 X 18 cm, approx.) fastened back-to-back and ballasted to hang vertically in the water column. Five replicate traps were evenly spaced along a 1.5 m length of PVC pipe to form a horizontal array; each array was attached to a buoyed anchor line and suspended horizontally in the water column at a depth of approximately 1 m in nearshore areas of about 10 m total depth. Arrays were deployed fortnightly at the commencement of spring and neap tide periods from February through late July, 2001. Arrays were retrieved after 3 days, and the contents of each trap were identified according to taxonomic group and larval stage, and counted.

Intertidal and subtidal data were analyzed separately. Count data for all taxonomic groups and developmental stages were summed within sites across all sampling dates, then normalized by dividing by the total number of larvae obtained across all sites and sampling dates. The resulting values provide an index of site-specific larval settlement over the sampling period. Relationships between larval settlement and drift card accumulations were tested by correlation analysis of arcsin transformed data. Rare species, defined here as those occurring in less than 2% of the samples, were excluded from the analysis.

Species Richness Estimation. Intertidal species richness was estimated at 15 rocky intertidal sites within the San Juan Channel and along the eastern shore of Haro Strait. Sites were chosen to span the range of drift card accumulations within these areas and were matched as closely as possible for substrate type and slope. Sites were visited on daytime low tides in July and August 2000. At each site, five vertical (cross-shore) transects were placed at random distances along a 12-meter length of shore. Seven randomly-spaced 25 X 25 cm quadrats were sampled along each vertical transect, for a total of 35 quadrats sampled/site. Presampling and construction of species-accumulation curves indicated that this sampling intensity was sufficient to detect more than 95% of macroscopic epibenthic taxa present within the site. Vertical transects spanned the intertidal from the highest (*Verrucaria*) zone to the lowest (Laminarian) zone. Because our goal was to detect differences in total species richness between sites, tidal height was not used as a factor in our analysis.

We used correlation analysis to test for relationships between species richness and drift card accumulations at all 15 sites for which we collected species richness data. In addition, we tested for correlations between species richness and larval settlement at subsets of 4 intertidal sites and 7 subtidal sites for which we had measures of both richness and settlement.

Results

The larval traps we deployed in intertidal and subtidal habitats are selective; that is, not all taxa find the traps equally attractive as settlement substrates. Therefore, resulting data provide a relative index of larval settlement for between-site comparisons only, and cannot be used to describe the entire larval pool present at any site. Larvae of crustaceans (crabs and shrimp), barnacles, gastropods, bivalves, polychaetes, and bryozoans were frequent in the samples; other invertebrate taxa were infrequent or absent entirely. The intertidal analysis reported here includes counts of barnacle cyprids and nauplii, bivalve veligers, crustacean nauplii, and polychaete larvae. The subtidal analysis reported here includes barnacle cyprids and nauplii, bryozoan larvae, crab zoea, crustacean nauplii, gastropod veligers, polychaete larvae, and shrimp zoea.

Larval settlement varied across taxa, sites, and dates. Bulk larval settlement (summed across the taxa and developmental stages indicated above, over the entire sampling period) showed a very weak positive correlation with drift card recoveries at intertidal sites, and a weak negative correlation at subtidal sites. Neither relationship was statistically significant (Table 1).

Table 1. Bulk larval settlement and drift card recoveries, by site. Top panel: intertidal sites; bottom panel: subtidal sites.

Intertidal Site	Percent larval abundance (untransformed)	Percent drift card recoveries (untransformed)	Correlation Coefficient (r)	Significance
Cedar Rock, Shaw Is	0.24	0.58	0.15	p=0.81
Hunt's Point, San Juan Is	0.10	0.25		
Point Caution North, San Juan Is	0.12	0.00		
Point Caution South, San Juan Is	0.26	0.08		
Point George, Shaw Is	0.28	0.08		

Subtidal Site	Percent larval abundance (untransformed)	Percent drift card recoveries (untransformed)	Correlation Coefficient (r)	Significance
Cedar Rock, Shaw Is	0.14	0.03	-0.34	p=0.42
Hunt's Point, San Juan Is	0.09	0.01		
Kings Point, Lopez Is	0.10	0.16		
Neck Point, Shaw Is	0.10	0.75		
Point Caution North, San Juan Is	0.12	0.00		
Point Caution South, San Juan Is	0.17	0.00		
Point George, Shaw Is	0.11	0.00		
Pear Point, San Juan Is	0.17	0.03		

Intertidal species richness appeared to be significantly negatively correlated with drift card recoveries (Table 2). However, this result was driven by a single site (Neck Point, Shaw Island). This site, which accumulated a greater number of drift cards than any other site in the study, was characterized by low species diversity attributable to dominance by a single non-native species. The abundance of this non-native species had the effect of depressing native species richness. Among the sites sampled, no others were dominated by non-native species. If we exclude this site from the analysis based on dominance by non-native species, the resultant correlation coefficient changes to -0.10 ($p=0.73$).

Table 2. Species richness vs. drift card recoveries

Site	Species Richness	Percent drift card recoveries (untransformed)	Correlation Coefficient (r)	Significance
Andrews Bay, San Juan Is	50	0.04	-0.68*	p=0.005**
Cattle Point East, San Juan Is	38	0.02		
Cattle Point West, San Juan Is	45	0.07		
Cedar Rock, Shaw Is	44	0.02		
Eagle Cove, San Juan Is	45	0.08		
Hunt's Point, San Juan Is	38	0.01		
Iceberg Point, Lopez Is	43	0.02		
Neck Point, Shaw Is	30	0.49		
Point Caution So., San Juan Is	42	0.00		
Point George, Shaw Is	44	0.00		
Reuben Tarte Park, San Juan Is	41	0.00		
San Juan Co Park, San Juan Is	45	0.02		
Shark Reef, Lopez Is	40	0.12		
South Point, Shaw Is	49	0.01		
Turn Island	40	0.11		

*Value changes to -0.10 with exclusion of data from Neck Point.

**Value changes to p=0.73 with exclusion of data from Neck Point

Species richness at intertidal sites appeared to be positively correlated with larval settlement, although the result was not statistically significant ($p>0.05$; Table 3). This result is based on a small sample size ($n=4$ sites). A larger sample size would increase statistical power and help resolve the relationship between these two variables. A weak positive correlation was observed between species richness and larval settlement at seven subtidal sites; this result was not statistically significant.

Table 3. Species richness vs. larval settlement for subsets of intertidal and subtidal sites. Top panel: intertidal sites; bottom panel: subtidal sites.

Intertidal Site	Species Richness	Percent larval abundance (untransformed)	Correlation Coefficient (r)	Significance
Cedar Rock, Shaw Is	44	0.24	0.93	0.07
Hunt's Point, San Juan Is	38	0.10		
Point Caution South, San Juan Is	42	0.26		
Point George, Shaw Is	44	0.28		

Subtidal Site	Species Richness	Percent larval abundance (untransformed)	Correlation Coefficient (r)	Significance
Cedar Rock, Shaw Is	44	0.14	0.40	0.38
Hunt's Point, San Juan Is	38	0.09		
Kings Point, Lopez Is	40	0.10		
Neck Point, Shaw Is	30	0.10		
Point Caution South, San Juan Is	42	0.17		
Point George, Shaw Is	44	0.11		
Pear Point, San Juan Is	40	0.17		

Discussion

Our results indicate that particle accumulations inferred from drift card studies appear to be poor indicators of the likelihood of larval settlement at spatial scales on the order of 1-10 km. Drift cards are coarse descriptors of Lagrangian transport and resultant particle accumulations. If larvae behave strictly as passive, surface-borne particles, one might expect them to accumulate in the same areas as drift cards. That no such patterns were observed indicates that larvae do not behave merely as passive surface-borne particles, that larval behavior plays a large role in determining settlement at small spatial scales, or that general patterns of larval settlement are not detectable at the scales we tested using the methods we employed. We found no evidence that rates of particle accumulation can be used to identify individual sites that are likely to experience high rates of larval settlement across multiple taxa. While this result may not be surprising in the context of larval biology, it is important in its demonstration that the coarse measures of transport and accumulation used here provide insufficient basis for making confident predictions about larval settlement for the purposes of reserve siting.

We observed high spatial and temporal variability in larval settlement across taxonomic groups and developmental stages. The existence of such variability suggests that development of reliable, inexpensive indicators of settlement may be difficult or impossible to achieve, at least for the suite of benthic invertebrate taxa considered here. More reliable predictions might be achieved for single species of interest. We do not address issues of single-species management here, and we stress that our results may not be fully applicable to issues of reserve siting or management of single species of unique conservation interest.

Species richness showed no positive correlation with particle accumulation, and no significant correlation with larval settlement. This finding implies that processes other than settlement determine community development at small spatial scales and that particle accumulation cannot be used as a surrogate for species accumulation.

Our results do not imply that physical oceanographic factors are unimportant to the successful design of MPA or MR networks. In the Georgia Basin/Puget Sound system, physical oceanographic factors are useful in determining, for example, sub-regions of high connectivity, likelihoods of connectivity between regions, sources of nutrient and larval inputs to each region, and foraging patterns and trophic dynamics (e.g., Shanks and Wright 1997; Dinnel et al. 1993; Klinger and Ebbesmeyer 2001; Zamon 2001). However, individual sites that provide especially high settlement value to MPA and MR networks may be difficult to identify from oceanographic data without considerable effort and cost. Therefore, we suggest that additional criteria for MPA and MR site choice be developed and implemented. These should be based on biologically or physically relevant metrics such as species composition or habitat complexity (e.g., Roberts et al. 2003 and references therein). Most importantly, the irreducible uncertainty associated with identifying sites of high functional value vis-à-vis larval settlement argues for implementation of a bet-hedging strategy in choosing and designating reserve sites within the Georgia Basin/Puget Sound region.

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Literature Cited

- Allison, G.W., J. Lubchenco, and M.H. Carr, 1998, Marine reserves are necessary but not sufficient for marine conservation. *Ecol Appl*, **8**: 79-92.
- Castilla, J.C., and M.A. Vargas, 1998, A plankton trap for exposed rocky intertidal shores, *Mar Ecol Prog Ser*, **175**:299-305.
- Dinnel P.A., D.A. Armstrong, and R.O. McMillan, 1993, Evidence for multiple recruitment-cohorts of Puget Sound Dungeness crab, *Cancer magister*, *Mar Biol*, **115**: 53-63.
- Roberts, C.M. et al., 2003, Application of ecological criteria in selecting marine reserves and developing reserve networks, *Ecol Appl* **13** Suppl: S215-S228.
- Shanks, A.L., and W.G. Wright, 1987, Internal-wave-mediated shoreward transport of cyprids, magalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles, *J Exp Mar Biol Ecol*, **114**: 1-13.
- Wing, S.R., L.W. Botsford, J.L. Largier, and L.E. Morgan, 1995, Spatial structure of relaxation events and crab settlement in the northern California upwelling system, *Mar Ecol Prog Ser*, **128**:199-211.
- Zamon, J.E., 2001, Seal predation on salmon and forage fish schools as a function of tidal currents in the San Juan Islands, WA, USA, *Fisheries-Oceanography*, **10**: 353-366.